Synchronization of Bursting Neurons: What Matters in the Network Topology

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We study the influence of coupling strength and network topology on synchronization behavior in pulse-coupled networks of bursting Hindmarsh-Rose neurons. Surprisingly, we find that the stability of the completely synchronous state in such networks only depends on the number of signals each neuron receives, independent of all other details of the network topology. This is in contrast with linearly coupled bursting neurons where complete synchrony strongly depends on the network structure and number of cells. Through analysis and numerics, we show that the onset of synchrony in a network with *any* coupling topology admitting complete synchronization is ensured by one single condition.

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Synchronized neuronal firing has been suggested as particularly relevant for neuronal signal transmission and coding. While its involvement in cortical processing is somewhat controversial, the presence of synchronization has been shown in special areas such as the olfactory system or the hippocampal region [1]. Model studies of neuronal synchronization can be separated in those where threshold models of the integrate-and-fire type are used [2] and those where conductance-based spiking and bursting models are employed [3]. Bursting occurs when neuron activity alternates, on a slow time scale, between a quiescent state and fast repetitive spiking. There has been much work on mechanisms that produce such bursting [4]. In contrast to coupled spiking neurons, whose synchronous dynamics is relatively simple, interacting bursting neurons may exhibit different forms of synchrony; including synchronization of individual spikes, burst synchronization when only the envelopes of the spikes synchronize, and complete synchrony [5]. Typically, burst synchronization arises at a low coupling strength whereas complete synchrony, which involves both burst and spike synchronization regimes, requires a stronger coupling. Models of interacting bursting neurons often use one of two different forms of coupling depending on whether the synapse is electrical or chemical. In the first case, the coupling through gap junctions is linear and directly dependent on the difference of the membrane potentials. In the second case, the coupling is pulsatile and often modeled as a static sigmoidal nonlinear input-output function with a threshold and saturation [6]. One important question about interacting bursting neurons with such linear and pulsatile couplings is that of complete synchronization: What are the conditions for the stability of the completely synchronous state, especially with respect to coupling strengths and coupling configurations of the network? This problem was intensively studied for linearly coupled networks of bursting neurons [7,8], and more generally, of limit-cycle and chaotic oscillators [9,10]. In particular, it has been shown that synchrony in such networks strongly depends on the structure and size of the network.

The purpose of this Letter is to report a surprising find regarding the synchronization of synaptically coupled networks of bursting neurons. Studying a network of pulse-coupled Hindmarsh-Rose (HR) neurons [11], we discovered that all that matters for the onset of complete synchrony is the number of signals, k, received by each neuron. This is independent of all other details of the network structure. More precisely, the synchronization threshold is inversely proportional to the number of incoming signals k. This criterion applies to a neuronal network with *any* coupling topology admitting complete synchrony. For this property to be true, each neuron must receive signals from k others, where k is uniform for all neurons. In this work, we concentrate on networks of HR neurons exhibiting square-wave bursting, which is very resistant to synchronization. The single HR model can be linearly transformed into the form $\dot{x} = ax^2 - x^3 - y - z$, $\dot{y} = (a + \alpha) \times x^2 - y$, $\dot{z} = \mu(bx + c - z)$, where x represents the membrane potential, and y and z are associated with fast and slow currents, respectively. Hereafter, the parameters are chosen and fixed as follows: $a = 2.8$, $\alpha = 1.6$, $c = 5$, $b = 9$, $\mu = 0.001$. Consider now a network of n synaptically coupled HR models. The equations of motion are the following:

$$\dot{x}_i = ax_i^2 - x_i^3 - y_i - z_i - g_s(x_i - V_s)\sum_{j=1}^{n} c_{ij}\Gamma(x_j),$$
$$\dot{y}_i = (a + \alpha)x_i^2 - y_i, \qquad \dot{z}_i = \mu(bx_i + c - z_i), \qquad (1)$$
$$i, j = \overline{1, n}.$$

Here, the neurons are identical and the synapses are fast and instantaneous. The parameter g_s is the synaptic coupling strength. The reversal potential $V_s > x_i(t)$ for $\forall\ x_i$ and $\forall\ t$, i.e., the synapse is excitatory. The synaptic coupling function is modeled by the sigmoidal function $\Gamma(x_j) = 1/[1 + \exp\{-\lambda(x_j - \Theta_s)\}]$ (a limiting version of $\Gamma(x_j)$ is the Heaviside function). This oft-used coupling form was called fast threshold modulation by Somers and Kopell [6]. The threshold Θ_s is chosen such that every spike in the single neuron burst can reach the threshold (see Fig. 1). Hereafter, $\Theta_s = -0.25$ and $V_s = 2$.

$\mathbf{C} = (c_{ij})$ is the $n \times n$ connectivity matrix: $c_{ij} = 1$ if neuron i is connected to neuron j, $c_{ij} = 0$ otherwise, and $c_{ii} = 0$. Matrix $\mathbf{C}$ can be asymmetric such that both mutual and unidirectional couplings are allowed. We require equal row sums $k = \sum_{j=1}^{n} c_{ij}$, $i = 1, \ldots, n$. This requirement is a necessary condition for the existence of the synchronous solution, namely, the invariance of hyperplane $D = \{\xi_1(t) = \xi_2(t) = \cdots = \xi_n(t)\}$, $\xi_i = (x_i, y_i, z_i)$, and $i = \overline{1, n}$. In fact, the equal row-sum property implies a network where each cell has the same number k of inputs from other neurons. Synchronous behavior on the manifold D is generated by the system:

$$\begin{aligned} \dot{x} &= ax^2 - x^3 - y - z - kg_s(x - V_s)\Gamma(x), \\ \dot{y} &= (a+\alpha)x^2 - y, \qquad \dot{z} = \mu(bx + c - z). \end{aligned} \tag{2}$$

Introducing the differences between the neural oscillator coordinates $\xi_{ij} = x_j - x_i$, $\eta_{ij} = y_j - y_i$, $\zeta_{ij} = z_j - z_i$, $i, j = 1, \ldots, n$ in the limit when these differences are infinitesimal, we derive the stability equations for the transverse perturbations to the synchronization manifold D:

$$\begin{aligned} \dot{\xi}_{ij} &= (2ax - 3x^2)\xi_{ij} - \eta_{ij} - \zeta_{ij} - kg_s\Gamma(x)\xi_{ij} \\ &\quad + g_s(V_s - x)\Gamma'_x(x)\Big(k\xi_{ij} + \sum_{h=1}^{n}\{c_{jh}\xi_{jh} - c_{ih}\xi_{ih}\}\Big), \\ \dot{\eta}_{ij} &= 2(a+\alpha)x\xi_{ij} - \eta_{ij}, \qquad \dot{\zeta}_{ij} = \mu(b\xi_{ij} - \zeta_{ij}). \end{aligned} \tag{3}$$

The derivatives are calculated at the point $\xi = 0$, $\eta = 0$, $\zeta = 0$, and $\{x(t), y(t), z(t)\}$ corresponds to the synchronous bursting solution defined via system (2). The first coupling term $S_1 = -kg_s\Gamma(x)\xi_{ij}$ accounts for the number of inputs k. At the same time, the contribution of the second coupling term $S_2 = g_s(V_s - x)\Gamma'_x(x)(\cdot)$ depends on the coupling configuration. Note that the term $\sum_{h=1}^{n}\{c_{jh}\xi_{jh} - c_{ih}\xi_{ih}\}$ is the same as for linear coupling [9]. In terms of the original variables x_i, the corresponding coupling matrix $\mathbf{G} = \mathbf{C} - k\mathbf{I}$ is the Laplacian of the connected graph, except for a sign change. It is well known that $\mathbf{G}$ has one zero eigenvalue γ_1 and all other eigenvalues have nonpositive real parts. If the coupling is mutual, $\mathbf{G}$ is symmetric and all eigenvalues are real. For simplicity, suppose that the eigenvalue γ_2 with the largest real part is simple. Then, applying the linear transformation that diagonalizes $\mathbf{G}$ to Eq. (3), we obtain the stability equation for the most unstable transverse mode:

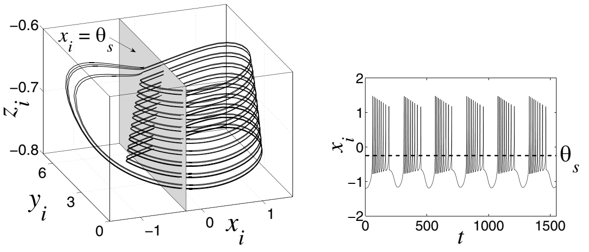

FIG. 1. The synaptic threshold Θ_s and square-wave bursting of the HR model (left). The corresponding time series (right).

$$\begin{aligned} \dot{\xi} &= (2ax - 3x^2)\xi - \eta - \zeta - \Omega(x)\xi, \\ \dot{\eta} &= 2(a+\alpha)x\xi - \eta, \qquad \dot{\zeta} = \mu(b\xi - \zeta), \end{aligned} \tag{4}$$

where $\Omega(x) = kg_s\Gamma(x) - g_s(V_s - x)\Gamma'_x(x)(k + \gamma_2)$. System (4) is an analog of the Master Stability function [9] for synaptically coupled networks (1). If γ_2 is not simple, then we can write similar equations to system (4) for the vectors spanning the corresponding blocks in the Jordan normal form of $\mathbf{G}$. The stability discussion, however, is essentially the same. Consider now its application to basic network configurations.

Globally coupled networks.—In this case, $\gamma_2 = -n$ and $k = n - 1$. Consequently, $\Omega(x) = kg_s\Gamma(x) + g_s(V_s - x)\Gamma'_x(x)$. The function $\Gamma(x)$ together with its derivative $\Gamma'_x(x)$ is non-negative, and $(V_s - x)$ is always positive (the synapses are excitatory). Therefore $\Omega(x)$ is always non-negative and the coupling term $-\Omega(x)\xi_{ij}$ aims at stabilizing the zero equilibrium of system (4); corresponding to the synchronous solution. The function $\Omega(x)$ strongly depends on whether the membrane potential $x(t)$ exceeds the threshold Θ_s or not. In fact, kg_s is a lower bound of $\Omega(x)$ in the region $x(t) > \Theta_s$ and strongly contributes to the stability. At the same time, when $x(t)$ is below Θ_s, the first term in $\Omega(x)$ rapidly decreases to zero, and the second coupling term becomes decisive in a small region close to $x = \Theta_s$. This region is defined by the parameter λ [see Fig. 2 (left panel)]. Applying the Lyapunov function method to the stability of system (4), similar to [10], we prove that the synchronous state can be made stable, provided the coupling g_s is sufficiently strong. The analysis shows that the major part of the quiescent (slow) mode of the synchronous solution, where the contribution of $\Omega(x)$ is negligible, lies in a stable zone. Here, the derivative of the Lyapunov function is always negative, i.e., where the solutions of the individual systems converge to each other. On the other hand, the part of the bursting

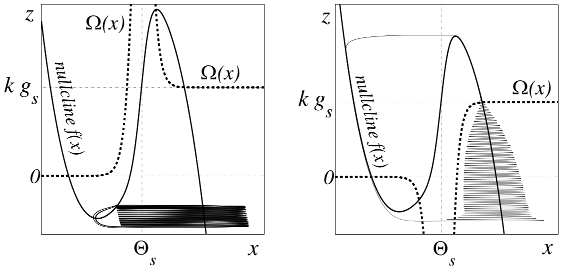

FIG. 2. The function $\Omega(x)$ and the corresponding synchronous bursting. Globally coupled HR neurons ($k = n - 1$, $\lambda = 10$) (left). Ring of locally coupled HR neurons ($k = 2$, $\lambda = 10$) (right).

solution that is the most difficult to synchronize favorably lies in the region $x(t) \geq \Theta_s$, where the contribution of $\Omega(x) = kg_s$ is strong and depends on k. Similarly, we prove that the remaining spiking part of the synchronous solution for $x(t) \leq \Theta_s$ can be stabilized by increasing g_s under the constraint that $\Gamma(x)$ is not the Heaviside function (λ is not too large). Hereafter, we postpone the detailed proof [12] and give only the main result. Our stability conditions give the following estimate for the synchronization threshold:

$$g_s^* = g_s^{(n=2)}/k, \tag{5}$$

where $k = n - 1$ and $g_s^{(n=2)}$ is a constant corresponding to the synchronization coupling threshold between two mutually coupled HR neurons ($k = 1$). The constant $g_s^{(n=2)}$ comes from sufficient conditions and therefore gives an overestimate for the real coupling strength that leads to complete synchronization of two HR neurons: 2.94 predicted versus 1.285 actual for the above mentioned parameters and $\lambda = 10$. However, using the numerically obtained $g_s^{(n=2)}$, we can predict the threshold g_s^*, for any k, from Eq. (5), as shown in the numerical examples below.

Densely coupled networks.—The eigenvalue γ_2 of $\mathbf{G}$ for such networks is very close to $-k$. For example, for a ring of $2K$-nearest-neighbor mutually coupled neurons, $\gamma_2 = -4\sum_{l=1}^{K} \sin^2 \frac{l\pi}{n}$ [13] with $n = 10$, $K = 4$, and $k = 2K = 8$, we obtain $\gamma_2 \approx -7.976$. Consequently, the function $\Omega(x)$ becomes close to $kg_s\Gamma(x)$. Therefore, if k is sufficiently large, the bound for the synchronization threshold will be nearly identical to that for globally coupled networks.

Intermediately and sparsely coupled networks.—When the number of links between the neurons in a network is small, the eigenvalue γ_2 is also small such that the second term in $\Omega(x)$, $-g_s(V_s - x)\Gamma_x'(x)(k + \gamma_2)$ no longer favors the stability. Consequently, the function $\Omega(x)$ takes negative values in the region close to the threshold Θ_s and defines the instability zone, where the coupling desynchronizes the neurons. At the same time, the stability zone is defined by the first term in Ω, $kg_s\Gamma(x)$, which is bounded from below by kg_s in the region $x(t) \geq \Theta_s$ [cf. Figure 2 (right panel)]. Strictly speaking, while we are no longer able to prove that the systems synchronize within the framework of the Lyapunov function method, the slow-fast structure of Eqs. (1) and (2) yields the following. The excitatory coupling raises the x nullcline $f(x) = -\alpha x^2 - x^3 - kg_s(x - V_s)\Gamma(x)$ of system (2) such that the right-branch attractor corresponding to spiking gradually moves to the right from the threshold $x = \Theta_s$. Finally, it leaves the zone where $\Omega(x)$ is negative (cf. Figure 2 (right)), provided g_s is large enough. Note that the raising of the nullcline and the shift of the attractor are also governed by kg_s [cf. Equation (2)]. In the singular perturbation limit ($\mu \rightarrow 0$), the synchronous trajectory traverses the instability region via fast jumps from the quiescent mode to repetitive spiking, and spends almost all its time in the stability regions. As in the case of the global coupling, the first stability zone corresponding to a major part of the slow motion along the left branch of $f(x)$ is always stable, whereas the stability of the second zone corresponding to spiking is defined by kg_s. Hence, once again we see that condition (5) is a good estimate for the synchronization threshold in sparsely and intermediately connected networks. Consequently, the synchronization threshold in locally synaptically coupled networks is constant; $g_s^* = g_s^{(n=2)}/2$ for mutually nearest-neighbor coupled neurons, and does not depend on the number of neurons n. This is in sharp contrast with linearly coupled networks where the coupling required for stable synchronization has a quadratic dependence on n [10]. Collecting all the considered coupling topologies, we come to the following assertion.

Statement.—The synchronization threshold estimate (5) $g_s^* = g_s^{(n=2)}/k$ is valid for the networks (1) with any coupling configuration (whether global or local, regular or random, mutual or unidirectional) under the constraint that each neuron has the same number of inputs k.

In support of this claim, we determine numerically the threshold for complete synchronization as a function of k for various coupling configurations (local, intermediate, and global), and compare it to the value predicted by Eq. (5). For $g_s^{(n=2)}$, the value from simulation of two mutually coupled HR neurons was used. This value is $g_s^{(n=2)} = 1.285$ for $\lambda = 10$ and $g_s^{(n=2)} = 1.139$ for $\lambda = 50$. From the results shown in Fig. 3 it can be seen that the prediction is nearly perfect. Note that even for large λ, when the synaptic function $\Gamma(x_i)$ approaches the Heaviside function, the estimate (5) gives an excellent numerical prediction.

To illustrate the power of condition (5) even further we have simulated—in addition to the regular, mutually coupled networks from Fig. 3—a series of randomly generated *unidirectionally* coupled networks of HR neurons with uniform number of synapses as those shown in Fig. 4. For all simulated networks, numerical results are nearly identical to the analytical predictions of Eq. (5).

Finally, we have tested robustness of the synchronization with respect to a mismatch in the synaptic strengths.

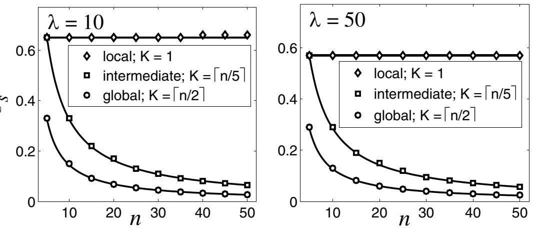

FIG. 3. Synchronization thresholds g_s^* in a ring of $2K$-nearest-neighbor coupled HR neurons as functions of n for various coupling configurations (different K). Markers: Simulation results. Solid line: Prediction of Eq. (5).

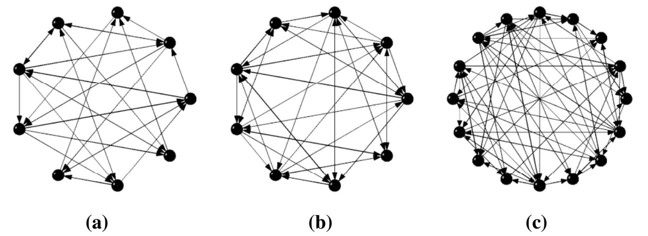

FIG. 4. Ten networks of each type, (a) $n = 9$, $k = 3$; (b) $n = 9$, $k = 4$; (c) $n = 16$, $k = 4$, were generated randomly. The synchronization threshold for networks of type (a): $g_s^* = 0.429$ for $\lambda = 10$, and $g_s^* = 0.380$ for $\lambda = 50$; and of types (b) and (c): $g_s^* = 0.322$ for $\lambda = 10$, and $g_s = 0.285$ for $\lambda = 50$. All the calculated thresholds coincide perfectly with $g_s^{(n=2)}/k$.

We have simulated networks of 20 neurons for the local, intermediate, and global cases, introducing a mismatch in the synaptic strengths around the average g_s. Perfect synchronization is no longer possible in these cases, due to the absence of the synchronization manifold, and there is always an error in the synchronization. However, for a given value of g_s this error falls rapidly and then remains constant when g_s is further increased. This point can be seen as the coupling threshold for the approximate synchronization. In all simulated cases this value is nearly identical to the synchronization threshold without mismatch as shown in Fig. 3. The synchronization has been verified to be robust for mismatches in g_s of up to 5%.

The derivation of condition (5) mainly relies on two properties of the coupled system: (i) the spiking state, which is most resistant to synchronization, encircles the right branch of the fast nullcline $f(x)$, where the contribution of coupling is strong; (ii) the quiescent state, which is easy to synchronize, belongs to the left branch of $f(x)$. These properties are typical for square-wave and parabolic bursters, whose formation involves the two branches of $f(x)$. Consequently, the synchronization condition (5) is not restricted to the HR neuron, but is applicable to other Hodgkin-Huxley-type neurons, exhibiting square-wave and parabolic bursters. For example, two Sherman models displaying square-wave bursting for the standard parameters [7], synchronize at $g_s^{(n=2)} = 0.25$ when synaptically coupled with $\Theta_s = -40$, $V_s = -10$, and $\lambda = 50$. The synchronization thresholds in a larger network (1) of the Sherman models correspond to the values predicted by $g_s^{(n=2)}/k$.

In summary, the single condition (5) ensures the onset of complete synchronization in networks of synaptically coupled bursting neurons (1) with any coupling topology in which each neuron receives signals from k others. The synchronization condition depends on the number of inputs k and *not* on the connectivity matrix. The equal k constraint is often invalid for biologically relevant networks with a complex structure where the number of inputs is not necessarily constant, but if k is uniform for a group of neurons, synchronization within this group of neurons can occur. The synaptic strengths can also change as a result of pre- and post-synaptic cell activity such that the inputs to the neurons become equal only for a specific interval of time, resulting in temporal approximate synchronization. This work promises to allow an analytical treatment of even temporal synchrony in bursting cells.

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